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RESEARCH ARTICLE

Occupancy dynamics of rare cyprinids after invasive fish eradication

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Abstract

1. The eradication of invasive species is a management strategy implemented to eliminate adverse impacts of invaders on native species communities. After eradications, follow-up studies are done to confirm eradication of the invasive species and the short-term recovery of the native species, but long-term monitoring to confirm full population recovery and stability is often not completed.
2. In this study, long-term monitoring of native fishes was carried out over 5 years after the eradication of an invasive fish from the Rondegat River, South Africa. Forty-six sites distributed along four river sections were sampled for presence/absence using underwater cameras and snorkel surveys. Density data were collected by snorkel surveys.
3. Using multi-season occupancy models, the annual probability of colonization and local extinction of the native fishes and annual rate of change in occupancy along the river were estimated. Changes in native fish densities across time and across the control and treatment sections were analysed using Kruskal–Wallis analysis, followed by Dunn's post-hoc test.
4. Probability of colonization and local extinction differed for each native fish species and may have been affected by extrinsic factors, such as rainfall, and intrinsic density-dependent factors, hypothesized from the density data. The occupancy rates of change revealed that the two Near Threatened fish species have reached an occupancy dynamic equilibrium but the Endangered fish has not, suggesting that other conservation efforts may be needed.
5. Long-term monitoring of native fishes after an eradication programme has confirmed the successful removal of the invader and the recovery and stability of the community. However, successful eradication was not sufficient for full recovery of all species; additional conservation management strategies are needed to secure the population stability and persistence of endangered fishes. We recommend that eradication programmes, regardless of locality, should employ long-term monitoring to ensure full recovery of a native fish community.

KEYWORDS

alien species, fish, monitoring, rare species, recolonization, river

1 | INTRODUCTION

Invasive species are among the greatest threats to native species, causing declines in population numbers and extinctions (Clavero & García-Berthou, 2005). As a result, conservation agencies may resort to eradication programmes that target the removal of invasive species in the hope that native populations can escape extirpation and recover (Lampert, Hastings, Grosholz, Jardine, & Sanchirico, 2014; Simberloff et al., 2013). To evaluate the success of these eradication attempts, sites are resampled to confirm eradication of the invasive species and to assess the response of the native species; however, this is not often undertaken on a long-term basis to confirm population persistence and stability (Rytwinski et al., 2019).

Because fish species exhibit different life histories and, consequently, are affected differently by modifications to their natural environment, long-term patterns of colonization and local extinction should be explored to understand how populations recover after habitat rehabilitation (Rytwinski et al., 2019). Investigating the dynamics of vital rates is important to understand the persistence of the population, classically through a balance between colonization and local extinctions driven by stochastic processes and distribution patterns of the species (Hanski, 1998). However, the persistence of a population may also be driven by density-dependent processes; smaller populations tend to have higher probabilities of extinctions that, for rare species, can be exacerbated by extrinsic/deterministic factors such as habitat degradation or introduction of a predator/competitor (Ovaskainen & Saastamoinen, 2018; Thomas, 1994). Mitigating such detrimental factors should result in colonization of these open and improved habitats. A species' ability to respond to these changes in the environment should result in persistence of these rare species (Thomas, 1994). Hence, to confirm persistence, long-term monitoring programmes should be implemented to track the species' response to habitat rehabilitation.

To track species movements throughout the landscape, ecologists must first be able to detect them. Rare and cryptic species may be hard to detect in the field, increasing the potential for false negatives, which would bias estimates of colonization and local extinction probabilities; therefore, the detectability of the species must be considered (MacKenzie et al., 2018a). Occupancy modelling is a statistical technique that estimates the probability of occupancy of a species when accounting for imperfect detection and, extending from simple single-season to multi-season models, estimates the probability of colonization and local extinctions across time (Falke, Bailey, Fausch, & Bestgen, 2012; MacKenzie, Nichols, & Hines, 2003). The multi-season occupancy modelling approach estimates the probability of occupancy, colonization, and local extinction while taking into account the detectability of a species, reducing false negatives (MacKenzie et al., 2003).

One eradication project that included long-term monitoring was conducted in the Rondegat River, South Africa, a tributary to the Olifants River that drains into the Clanwilliam Dam (Figure 1). Smallmouth bass, *Micropterus dolomieu* Lacepède 1802, and other centrarchids were intentionally introduced in the catchment via stocking programmes (Weyl, Ellender, Woodford, & Jordaan, 2013; Weyl, Finlayson, Impson, Woodford, & Steinkjer, 2014). The Rondegat River has subsequently experienced declines and, in some cases, the extirpation of native fishes, including several endemic species, including Clanwilliam redfin *Sedercypris calidus* (Barnard 1938) and fiery redfin *Pseudobarbus phlegethon* (Barnard 1938) in invaded sections (Weyl et al., 2013; Woodford, Impson, Day, & Bills, 2005). In 2012, rotenone was applied to the river in an attempt to eradicate smallmouth bass, and the treatment was repeated to ensure full eradication in 2013

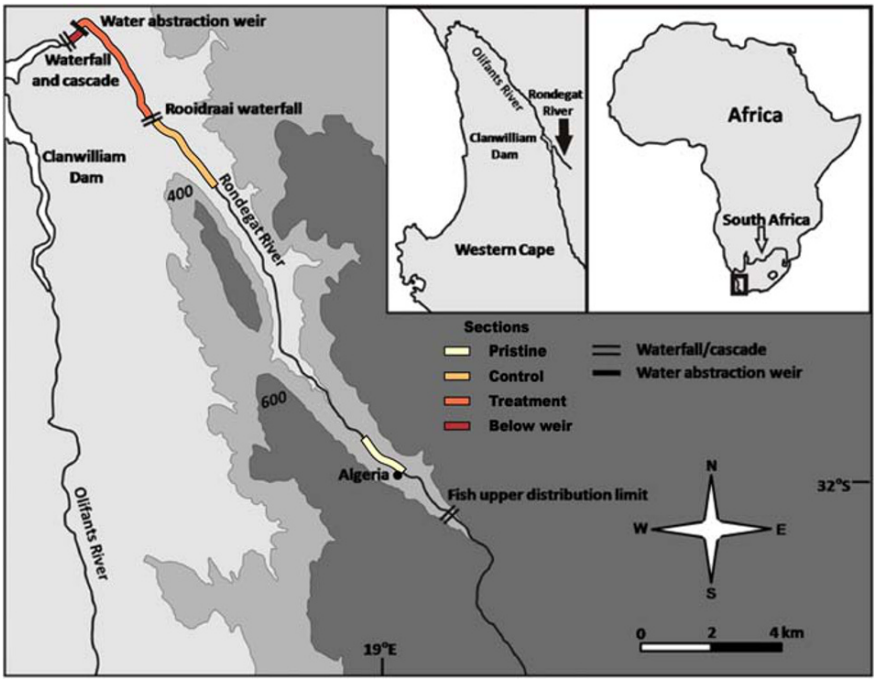

FIGURE 1 Rondegat River with experimental sections identified. Modified from Weyl et al. (2013)

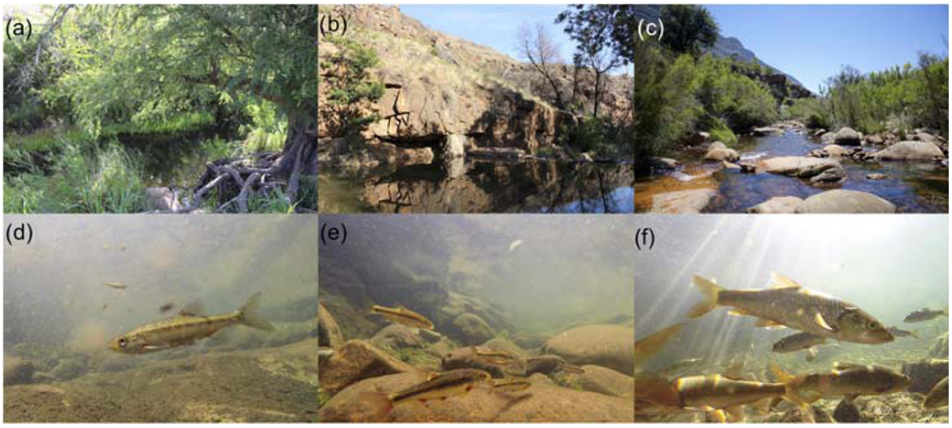

FIGURE 2 Photographs of the Rondegat River and its endemic fishes: (a) site in the pristine section; (b) site in the control section; (c) site in the treatment section; (d) Clanwilliam redfin *Sedercypris calidus*; (e) fiery redfin *Pseudobarbus phlegethon*; (f) Clanwilliam yellowfish *Labeobarus seeberi*. Photographs: Rowshyra Castañeda

(Weyl et al., 2014). In the year following the removal of smallmouth bass after the first rotenone treatment, there was an increase in the native fish distribution downstream (Weyl et al., 2014).

In this study, multi-season occupancy models were used to estimate the annual probability of colonization and local extinction of rare endemic fishes across pools in the Rondegat River (Figure 2a–c) after the eradication of invasive species. The endemic fishes are Clanwilliam redfin assessed by the International Union for Conservation of Nature (IUCN) Red List as Near Threatened (Van der Walt, Jordaan, & Impson, 2017), fiery redfin assessed as Endangered (Van der Walt, Impson, & Jordaan, 2017), and Clanwilliam yellowfish *Labeobarbus seeberi* (Gilchrist & Thompson 1913) assessed as Near Threatened (Impson, Van der Walt, & Jordaan, 2017) (Figure 2d–f). All three fishes have been adversely affected by the invasion of smallmouth bass and other black basses (van der Walt et al., 2019), and understanding their colonization potential and local extinction patterns after eradication is crucial to predicting long-term native fish population responses to invasive fish removal and to inform similar interventions in other rivers and future conservation management strategies, such as habitat restorations (Rytwinski et al., 2019).

2 | METHODS

2.1 | Study site

The Rondegat River is a 28 km shallow headwater stream that runs through the Cederberg mountains to its confluence with the Olifants River at the Clanwilliam Dam (Weyl et al., 2013). The Rondegat River catchment receives, on average, 800 mm of rainfall per annum and is used for human services, such as water abstraction for agricultural, household, and recreational purposes (Woodford et al., 2005). The river is very clear (0.5–2.8 NTU), ideal for non-invasive visual sampling methods such as underwater cameras and snorkel surveys. Natural and artificial barriers to invasion within the river have been used to classify it into four sections that represent the different experimental sections: pristine, control, treatment, and below weir. The pristine section is a 1.5 km stretch within the upper limit of the fishes' distributions, the control section is a 3 km stretch just upstream of the Rooidrai waterfall, the treatment section is a 2.5 km stretch where the rotenone treatment was applied from the Rooidrai waterfall to a water diversion weir, and the below-weir section is a 2.5 km stretch where the current invasion front is located (Figure 1). The water-diversion weir is an artificial barrier to upstream invasions by various non-native fishes, including banded tilapia *Tilapia sparrmanii* Smith 1840, bluegill *Lepomis macrochirus* Rafinesque 1819, largemouth bass *Micropterus salmoides* (Lacepède 1802), and smallmouth bass. The presence of smallmouth bass above the weir to the Rooidrai waterfall, a natural barrier to upstream invasions, is a consequence of invasion prior to the construction of the weir (Weyl et al., 2013).

2.2 | Field collection

The rotenone treatment was conducted by CapeNature, the local nature conservation authority, following an environmental impact assessment (Impson, van Wilgen, & Weyl, 2013). Monitoring the impact and recovery of native fish populations was based on non-invasive methods (i.e. snorkelling and underwater video analysis) under CapeNature permit no. AAAOO4–00702-0035. Yearly monitoring of the fish distributions in the Rondegat River began in February 2011, and was conducted in February 2012 and 2013, a month prior to the rotenone treatments, which occurred in March (Weyl et al., 2014), and repeated every year in February until 2016. Sampling of 29 sites was completed in 2011, 40 sites in 2012, 44 sites in 2013, 39 sites in 2014, 45 sites in 2015, and 46 sites in 2016. Up to seven sites were sampled in the pristine section, nine sites in the control section, 22 sites in the treatment section, and eight sites in the below-weir section. The number of sites increased after 2011 to ensure greater coverage of the pools along the Rondegat River. If sites were too shallow (<30 cm), because of annual variation in water flow, they could not be sampled. The sites were sampled for fishes using snorkel surveys and underwater cameras, yielding two sampling surveys per site per year. Sampling occurred at approximately the same time every year (February/March). Snorkel surveys were conducted by performing two consecutive passes along the length of the pool, counting the fishes observed and then averaging the counts and converting to density (m^{-2}; Ellender, Weyl, & Swartz, 2011; Weyl

et al., 2013). Underwater cameras (GoPro Hero) were placed at the downstream portion of the site in the deepest part facing upstream and were left to record video footage for 30 min (Ellender, Becker, Weyl, & Swartz, 2012). All video footage was viewed, and the occurrence of each species was noted.

2.3 | Statistical analysis

Owing to the non-parametric nature of the data and unmatched design (not every site could be sampled every year), the changes in mean native fish densities were analysed using a Kruskal–Wallis test (Kruskal & Wallis, 1952), followed by Dunn's pairwise comparison adjusting the *P*-value using the Holm method (Dunn, 1964). These analyses were performed using the dunn.test package in R (Dinno, 2017; R Core Team, 2019). The analysis was performed between the control section and the treatment area, and separately across time for the control section and the treatment section.

The probabilities of colonization and extinction across the different sections of the Rondegat River were estimated using multi-season occupancy models (MacKenzie et al., 2003, 2018b). These estimate the following: the probability ψ that a unit is occupied in the first season; the probability of colonization γ, which is the probability that a unit becomes occupied between seasons t and $t + 1$; the probability of extinction ε, which is the probability that a unit becomes unoccupied between seasons t and $t + 1$; and the detection probability p, which is the probability that a species is detected in an occupied site. The occupancy rate of change λ can then be calculated by dividing ψ_{t+1} by ψ_t (MacKenzie et al., 2003, 2018b).

A variety of models were tested using different combinations of the effect of year on colonization, extinction, and detection probability, along with the effect of stream section on colonization and extinction. The occupancy models were executed using the program PRESENCE (Hines & MacKenzie, 2018). Ranking of the candidate models was completed using the Akaike information criterion for small sample sizes (AIC_c), where the lowest AIC_c value was considered to be the best model, but all models with a difference in $AIC_c < 2$ support the hypothesis (Burnham & Anderson, 2002). In addition, the model-averaged estimates and standard deviations for all models were calculated. To understand which factors affect the probability of colonization and extinction, the best detection probability model when probability of occupancy was assumed to be constant was used.

3 | RESULTS

3.1 | Native fish densities in the treatment section increase and stabilize across time

The snorkel surveys revealed that the density estimations in the control section were not significantly different across the six years of sampling (Kruskal–Wallis, $P_{adj} > 0.50$) and the densities in the treatment section took varying lengths of time to reach approximately the same densities as the control for the Clanwilliam redfin and yellowfish, and to increase in both the control and treatment area for the fiery redfin (Figure 3). The Clanwilliam redfin densities in the treatment section were not significantly different from the control densities in 2015 and 2016 and did not differ between the two years (Kruskal–Wallis, $P_{adj} > 0.50$, Figure 3). The densities of the fiery redfin in the treatment section were not significantly different from the control section (Kruskal–Wallis, $P_{adj} > 0.10$); however, in 2015, the densities in the treatment section increased, albeit not significantly. Fiery redfin is generally quite rare in these two sections of the Rondegat River, with densities between 0 and 0.1 m^{-2} between 2011 and 2014. As of 2013, the Clanwilliam yellowfish treatment-section densities did not differ significantly from the control section and remained constant across the remaining sampling years (Kruskal–Wallis, $P_{adj} > 0.50$).

3.2 | Occupancy, colonization, and local extinction of the native fishes vary across time and space

The multi-season occupancy models showed that not all the native fishes are in equilibrium along the Rondegat River and that changes in occupancy result in annual variations in the probabilities of colonization and local extinctions. The effects of year and river section on the probabilities of colonization and local extinction vary for each native fish species. For all native fishes, their rate of change in occupancy λ depended on the previous year's occupancy, as the top models do not constrain the probabilities of colonization and local extinction (Table 1) (MacKenzie et al., 2018a). Of the multi-season occupancy models tested, two are supported for Clanwilliam redfin ($\Delta AIC_c < 2$; Table 1). For the top model, the probability of colonization varied by year and river section, whereas the probability of extinction was constant throughout years but varied across river section. For the fiery redfin, two multi-season occupancy models are supported ($\Delta AIC_c < 2$; Table 1). The top model reveals that the probability of colonization varied by year and river section, whereas the probability of extinction was constant throughout years and did not vary across river section. There are two multi-season occupancy models supported for Clanwilliam yellowfish ($\Delta AIC_c < 2$; Table 1). The top model reveals that the probability of colonization varied only by year, whereas the probability of extinction was constant throughout years and did not vary across river section.

3.3 | Treatment section experienced greatest changes in probability of colonization and occupancy

Before the rotenone treatment (2011–2012), the top models revealed that there was zero probability of colonization by all three native fishes in the treatment section where smallmouth bass was present. After the first rotenone treatment (2012–2013), the two redfins had an increase in probability of colonizing an unoccupied pool in the treatment section, and the Clanwilliam yellowfish had a

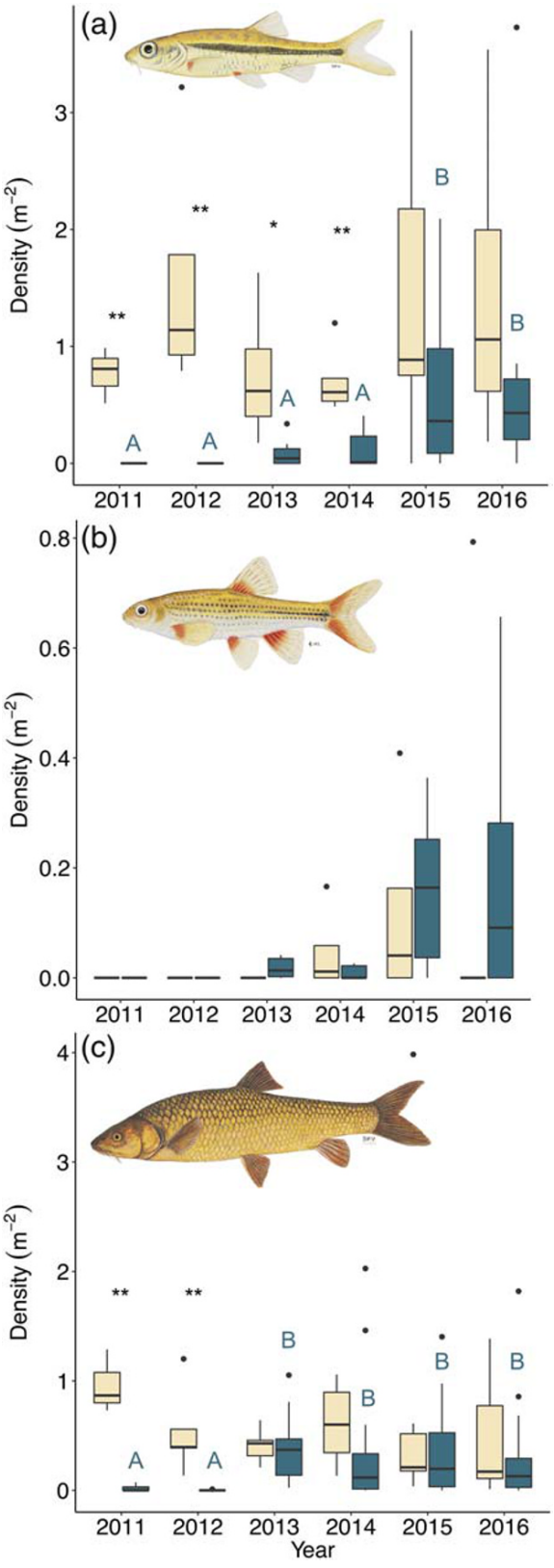

FIGURE 3 Boxplots of population densities (m^{-2}) of (a) Clanwilliam redfin, (b) fiery redfin, and (c) Clanwilliam yellowfish; control section in beige and the treatment section in blue. Asterisks represent significant differences between the control and treatment sections (*, $P < 0.05$; **, $P < 0.01$). Blue letters represent significant differences between years in the treatment section

river-wide increase in colonization probability (Table 2). The occupancy rate of change for all three fishes was $\lambda > 1$, indicating a significant increase in occupied pools in the treatment section (Table 3). In 2013, a month after the sampling, a second rotenone treatment was applied to the treatment section of the river to ensure the eradication of smallmouth bass; a post-treatment survey a few days after the rotenone application confirmed no fish presence, native or invasive, in the treatment section. One year after this second rotenone application (2013–2014), the top models indicated that the probability of colonization had dropped to $\gamma \approx 0$ for all three fishes (i.e. no unoccupied pool became occupied between sampling years), whereas the probability of local extinction ε was between 0.12 and 0.22 (i.e. occupied pools became unoccupied between sampling years; Table 2). Further, the occupancy rate of change, in the top models, dropped to between $\lambda = 0.8$ and 0.88 for all three native fishes, indicating that the fishes' occupancy of the treatment section for the redfins and river-wide for the Clanwilliam yellowfish had declined from the year before, but the treatment section was not completely unoccupied in 2014 (Table 3).

From 2014 to 2016, the occupancy dynamics seem to stabilize for the Clanwilliam redfin and yellowfish but not for the fiery redfin. The probability of colonization between the 2014 and 2015 sampling years from the top model was $\gamma = 0$ for both redfins in the treatment section, and $\gamma = 0.20$ for the Clanwilliam yellowfish river-wide (Table 2); however, the occupancy rate of change was $\lambda \approx 1$ for both the Clanwilliam redfin and yellowfish and $\lambda < 1$ for the fiery redfin (Table 3). From 2015 to 2016, there was a slight increase in the probability of colonization, greater than that of local extinction, for all three native fishes (Table 2), and the rates of change in occupancy were slightly above $\lambda = 1$ for the Clanwilliam redfin and yellowfish and significantly greater than $\lambda = 1$ for the fiery redfin.

3.4 | Redfins have varying occupancy dynamics in the pristine, control, and below-weir river sections

The probability of Clanwilliam redfin colonizing an unoccupied site was estimated to be $\gamma = 1$ for both the pristine and control sections for all years, except in the fourth year of colonization (from 2014 to 2015), when it dropped to $\gamma = 0$ for all sections. The below-weir section has zero probability of colonization. For the top model, the probability of local extinction, an occupied patch becoming unoccupied, was lowest in the pristine section and highest below the dam at the invasion front. The rates of change in occupancy λ vary across year and section, where the pristine and control sections have a high rate of change in the first year, and is likely to be an artefact of increased sampled sites with positive detections, and then remained around $\lambda = 1$ for the next 5 years (Table 3).

In the pristine section, the fiery redfin had a probability of colonization of $\gamma \approx 1$ for the second and fifth colonization years and, for all sections, $\gamma = 0$ for colonization years 3 and 4. The

TABLE 1 Summary of the multi-season occupancy model selection using the Akaike information criterion for small sample sizes (AIC_c) for the colonization and local extinction probabilities across the six sampling years for the three native fishes: Clanwilliam redfin, fiery redfin, and Clanwilliam yellowfish. The top 10 models are presented for each fish

Model ψ (2011), p (year)	AIC_c	ΔAIC_c	w_i	K	$-2\log(L)$
Clanwilliam redfin					
γ(year + section), ε(section)	369.04	0.00	0.5176	15	323.04
γ(year + section), ε(.)	369.82	0.78	0.3507	14	328.27
γ(section), ε(section)	372.63	3.59	0.0858	11	342.87
γ(section), ε(.)	373.99	4.95	0.0437	10	347.70
γ(section), ε(year + section)	380.98	11.94	0.0013	15	334.98
γ(section), ε(year)	382.64	13.60	0.0006	14	341.09
γ(year + section), ε(year + section)	384.61	15.57	0.0002	19	317.38
γ(year + section), ε(year)	384.80	15.76	0.0002	18	323.47
γ(.), ε(section)	393.57	24.53	0.0000	10	367.28
γ(year), ε(section)	394.61	25.57	0.0000	15	353.06
Fiery redfin					
γ(year + section), ε(.)	381.35	0.00	0.4966	14	339.8
γ(section), ε(.)	381.87	0.52	0.3835	10	355.58
γ(section), ε(section)	384.37	3.03	0.1094	11	354.61
γ(section), ε(year)	389.19	7.84	0.0099	14	347.64
γ(.), ε(section)	394.78	13.43	0.0006	10	368.49
γ(.)	401.01	19.66	0.0000	8	381.12
ε(.)	401.01	19.66	0.0000	8	381.12
γ(year + section), ε(year + section)	402.30	20.95	0.0000	19	335.07
γ(.), ε(.)	405.87	24.52	0.0000	9	382.87
γ(year), ε(.)	407.18	25.83	0.0000	13	369.80
Clanwilliam yellowfish					
γ(year), ε(.)	480.10	0.00	0.4182	13	442.72
γ(year), ε(section)	480.28	0.18	0.3816	14	438.73
γ(year + section), ε(.)	484.27	4.17	0.0519	14	442.72
γ(year + section), ε(section)	484.73	4.63	0.0412	15	438.73
ε(.)	484.76	4.67	0.0405	8	464.87
γ(.)	484.76	4.67	0.0405	8	464.87
γ(.), ε(.)	487.58	7.48	0.0099	9	464.58
γ(.), ε(region)	487.98	7.88	0.0081	10	461.69
γ(region), ε(.)	490.10	10.00	0.0028	10	463.81
γ(region), ε(region)	491.05	10.96	0.0017	11	461.29

Abbreviations: w_i, Akaike weights; K, number of parameters; L, Likelihood.

probability of colonization was highest after the first rotenone application (2012–2013) for the control section and negligible below the weir (Table 2). For the top model, the probability of extinction was constant across years and section. The rate of change in occupancy varied by section only between 2012 and 2013, where the control section had a high positive occupancy rate of change and then decreased to λ < 1 across the river over the next two years, to increase again to λ > 1 from 2015 to 2016 (Table 3).

3.5 | Model-averaged estimates of occupancy dynamics parameters across the river varies for each species

For the Clanwilliam redfin, the model-averaged estimates reveal that, overall, colonization was highest across the river after the first rotenone treatment (2012–2013) and the lowest in the fourth monitoring year (2014–2015, Table 4). Local extinction was highest across the river after the first rotenone treatment (2012–2013)

TABLE 2 Top multi-season occupancy model estimates of colonization ($\gamma_{year-year+1}$) and local extinction ($\varepsilon_{year-year+1}$) probabilities (*SD* in parentheses) for the three native fishes: Clanwilliam redfin, fiery redfin, and Clanwilliam yellowfish. Each top model had the probability of occupancy of the first sampling year (ψ_{2011}) and yearly differences in detection probability (p_{year})

	$\gamma_{2011-2012}$	$\gamma_{2012-2013}$	$\gamma_{2013-2014}$	$\gamma_{2014-2015}$	$\gamma_{2015-2016}$	ε
Clanwilliam redfin						
Pristine	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	0.00 (0.00)	1.00 (0.00)	0.03 (0.03)
Control	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	0.00 (0.00)	1.00 (0.00)	0.08 (0.04)
Treatment	0.00 (0.00)	0.59 (0.12)	0.06 (0.12)	0.00 (0.00)	0.27 (0.13)	0.21 (0.08)
Below weir	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.45 (0.22)
Fiery redfin						
Pristine	0.68 (0.22)	0.99 (0.01)	0.00 (0.00)[a]	0.00 (0.00)	0.97 (0.05)	—
Control	0.13 (0.12)	0.93 (0.06)	0.00 (0.00)[a]	0.00 (0.00)	0.70 (0.25)	—
Treatment	0.01 (0.02)	0.49 (0.11)	0.00 (0.00)[a]	0.00 (0.00)	0.14 (0.11)	—
Below weir	0.00 (0.00)[a]	0.06 (0.05)	0.00 (0.00)	0.00 (0.00)	0.01 (0.01)	—
River-wide	—	—	—	—	—	0.13 (0.05)
Clanwilliam yellowfish						
River-wide	0.00 (0.00)	0.70 (0.10)	0.00 (0.00)	0.20 (0.10)	0.52 (0.13)	0.17 (0.04)

[a]*SD* smaller than number of significant digits.

TABLE 3 Top multi-season occupancy model estimates (*SD* in parentheses) of the occupancy rate of change ($\lambda_{year-year+1}$) for the three native fishes: Clanwilliam redfin, fiery redfin, and Clanwilliam yellowfish. Each top model had the probability of occupancy of the first sampling year (ψ_{2011}) and yearly differences in detection probability (p_{year})

	$\lambda_{2011-2012}$	$\lambda_{2012-2013}$	$\lambda_{2013-2014}$	$\lambda_{2014-2015}$	$\lambda_{2015-2016}$
Clanwilliam redfin					
Pristine	4.06 (1.28)[b]	0.98 (0.02)	1.00 (0.00)[a]	—	1.03 (0.03)
Control		0.94 (0.03)	1.00 (0.00)[a]	—	1.09 (0.05)
Treatment	—	3.25 (1.06)	0.83 (0.10)	—	1.17 (0.21)
Below weir	—	0.55 (0.22)	0.55 (0.22)	—	0.55 (0.22)
River-wide				0.98 (0.03)	
Fiery redfin					
Pristine	11.91 (8.87)[b]	1.31 (0.44)	—	—	—
Control		5.39 (3.71)	—	—	—
Treatment	—	8.62 (5.56)	—	—	—
Below weir	—	2.08 (1.29)	—	—	—
River-wide	—	—	0.87 (0.05)	0.87 (0.05)	1.32 (0.19)
Clanwilliam yellowfish					
River-wide	0.83 (0.04)	1.56 (0.25)	0.83 (0.04)	0.95 (0.07)	1.18 (0.11)

[a]*SD* smaller than number of significant digits.
[b]Artefact of increased sampled sites within pristine and control sections with positive detections.

and the lowest in the fifth monitoring year (2015–2016, Table 4). The occupancy rate of change for Clanwilliam redfin varied yearly, with the highest rate of change after the first rotenone treatment (2012–2013), and remained around λ = 1 for 2014 and 2015, and slightly increased in 2016 (Figure 4a).

The model-averaged estimates of colonization probability for the fiery redfin were highest across the river after the first rotenone application (2012–2013) and equally low after the second rotenone application (2013–2014) and the year after (2014–2015, Table 4). Local extinction was highest across the river in the fourth year of colonization (2014–2015) and equally low in the second (2012–2013) and in the fifth years (2015–2016; Table 3). Rates of change in occupancy revealed similar trends as the top model, where the highest change in occupancy occurred after the first rotenone application, fell below λ = 1 for 2014 and 2015, to increase above λ = 1 in 2016 (Figure 4b).

For the Clanwilliam yellowfish, the model-averaged estimates showed that colonization was highest across the river after the

TABLE 4 Model-average estimates (*SD* in parentheses) of the probability of occupancy in the first year (ψ_{2011}), the probabilities of colonization ($\gamma_{year-year+1}$) and local extinction ($\varepsilon_{year-year+1}$), the detection probability (p_{year}), and the occupancy rate of change ($\lambda_{year-year+1}$)

	Clanwilliam redfin	Fiery redfin	Clanwilliam yellowfish
ψ_{2011}	0.25 (0.08)	0.06 (0.04)	0.64 (0.11)
$\gamma_{2011-2012}$	0.33 (0.46)	0.14 (0.24)	0.00 (0.00)
$\gamma_{2012-2013}$	0.63 (0.35)	0.57 (0.32)	0.72 (0.00)[a]
$\gamma_{2013-2014}$	0.36 (0.44)	0.02 (0.01)	0.00 (0.00)
$\gamma_{2014-2015}$	0.00 (0.00)	0.02 (0.01)	0.20 (0.00)[a]
$\gamma_{2015-2016}$	0.47 (0.40)	0.36 (0.35)	0.52 (0.00)[a]
$\varepsilon_{2011-2012}$	0.15 (0.10)	0.14 (0.00)[a]	0.34 (0.12)
$\varepsilon_{2012-2013}$	0.25 (0.14)	0.12 (0.00)[a]	0.17 (0.07)
$\varepsilon_{2013-2014}$	0.19 (0.13)	0.14 (0.00)[a]	0.21 (0.09)
$\varepsilon_{2014-2015}$	0.21 (0.13)	0.15 (0.00)[a]	0.22 (0.09)
$\varepsilon_{2015-2016}$	0.14 (0.09)	0.12 (0.00)[a]	0.17 (0.07)
p_{2011}	1.00 (0.00)	1.00 (0.00)	0.78 (0.09)
p_{2012}	0.46 (0.10)	0.24 (0.10)	0.69 (0.13)
p_{2013}	0.80 (0.07)	0.71 (0.07)	0.89 (0.04)
p_{2014}	0.86 (0.05)	0.68 (0.10)	0.90 (0.04)
p_{2015}	0.77 (0.09)	0.61 (0.12)	0.93 (0.04)
p_{2016}	0.89 (0.05)	0.68 (0.08)	0.81 (0.06)

[a]*SD* smaller than number of significant digits.

first rotenone application (2012–2013) and equally low in the first monitoring year (2011–2012) and after the second rotenone application (2013–2014; Table 4). Local extinction was highest across the river in the first monitoring year (2011–2012) and lowest after the first rotenone application (2012–2013; Table 4). The model-averaged estimates of the rates of change in occupancy indicate that the lowest rate was from 2011 to 2012 and the highest from 2012 to 2013, whereas the rates were close to λ = 1 in the third and fourth years of monitoring (Figure 4c).

4 | DISCUSSION

The probability of colonization for all three species varied yearly, suggesting that extrinsic drivers may be at play in the Rondegat River, which is a very dynamic system. Because of the human services that the river provides, it is subject to human modifications, through water abstraction and spread of invasive species, which are likely to affect colonization and local extinction probabilities. Further, the Cederberg mountains had irregular annual rainfall patterns across the study years, resulting in variation in habitat availability for the native fishes (Table 5).

The strongest driver of the occupancy dynamics of the native fishes was the presence of the invasive fish, smallmouth bass. In 2011–2012, there was no colonization of any native fish below the waterfall where smallmouth bass was present. Smallmouth bass and

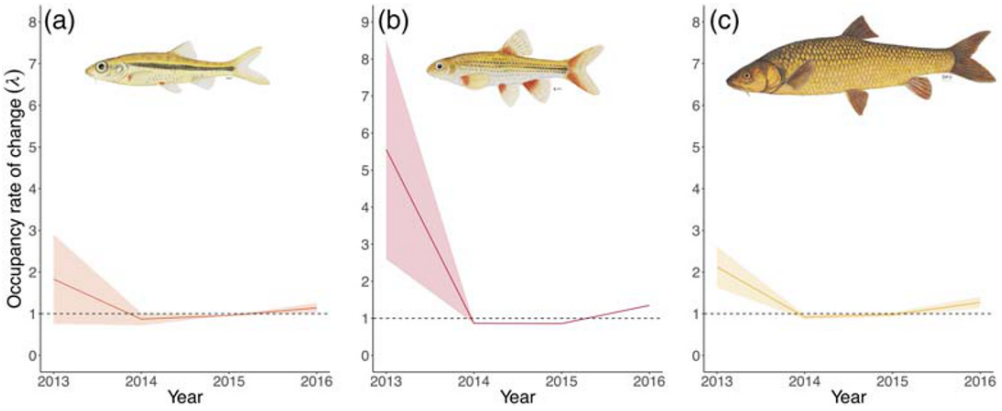

FIGURE 4 Annual model-averaged estimates and *SD*s of occupancy rates of change (calculated by dividing ψ_{t+1} by ψ_t) after the first rotenone treatment for each native fish: (a) Clanwilliam redfin (orange); (b) fiery redfin (red); (c) Clanwilliam yellowfish (yellow)

TABLE 5 Monthly rainfall (mm) at the Cederberg weather station between sampling periods provided by the South African Weather Service

	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Total
2011–2012	15.5	26.5	128.1	139.8	74	104.5	25.5	45	20.2	16.8	0	0	595.9
2012–2013	29	77	19.5	190	74	155	46.2	16	6.5	39	5	10	667.2
2013–2014	19	99.2	54.5	218.5	162.9	264.5	113.7	34.7	28.5	0	46.9	1	1043.4
2014–2015	40	21.8	75.5	133	134.5	100.5	36	3.7	71.5	0	13.3	2	631.8
2015–2016	10	1	8.4	153	118.5	30	17.8	9.6	7.5	3.5	32.3	0	391.6

other invasive centrarchids have been shown to contribute significantly to local extirpation of endemic fishes in South Africa, and their removal has led to the recovery of several native fishes (Ellender et al., 2018; van der Walt et al., 2019; van der Walt, Weyl, Woodford, & Radloff, 2016). Following the rotenone treatment to eradicate the invasive fishes in 2012, there was a marked increase in colonization and in occupancy of the treatment section for both Clanwilliam and fiery redfins, and overall for Clanwilliam yellowfish. Overall, the model-averaged estimates of the occupancy rates of change revealed that there was the highest positive change in occupancy after the first rotenone treatment. Thus, the distribution of these native fishes was strongly driven by negative interactions with smallmouth bass, as seen in other rivers in South Africa. The adverse effects of smallmouth bass are also reflected in the density data, where there was an increase in density in the treatment section for all native fishes and no difference in the control section for the Clanwilliam yellowfish (Weyl et al., 2014).

Although there was no significant difference in density pre and post-rotenone treatment for the two redfin species, it is important to note that density was greater than zero and there was an increase in occupancy. This indicates that the redfins occupied new pools in the treatment section after the first eradication attempt of smallmouth bass, albeit in small numbers. Further, fiery redfin was very rare in the Rondegat River, with no presences in the control section until 2014, probably because of its higher sensitivity to habitat degradation. Between 2010 and 2012, there was also physical removal of invasive trees along the banks of the river in the control and treatment sections, with no replanting of native plants and grasses, potentially decreasing habitat quality with increased sedimentation from runoff and increased water temperature from reduced shade (Bellingan et al., 2019; Impson et al., 2013). Native vegetation began to repopulate the riparian area of the Rondegat River in 2013 from seed banks in the soil (Impson et al., 2013), presumably increasing water and habitat quality in the control and treatment sections. In addition, there was a boom in chironomid density after 2013 (Bellingan et al., 2019), the dominant prey item for fiery redfin (Ellender, Wasserman, Chakona, Skelton, & Weyl, 2017), allowing the fiery redfin to colonize from the pristine section and survive, reproduce, and, thus, repopulate the control section by 2014. The positive effects of invasive tree removal on native fish density has also been shown in streams in Nevada, USA (Kennedy, Finlay, & Hobbie, 2005). Similar to our finding, a study on whether invasive fishes or habitat degradation were important drivers of fish diversity loss in Iberian streams found that invasive fishes were the strongest predictor of diversity loss (Hermoso, Clavero, Blanco-Garrido, & Prenda, 2011); however, habitat improvements also contributed to the increase in abundance of the fiery redfin. The removal of smallmouth bass and invasive trees had a positive impact on the native fish community.

The probability of colonization in the below-weir section was zero for Clanwilliam redfin and negligible for fiery redfin. The below-weir section may be outside of their natural range or the water-abstraction weir may impose a downstream colonization barrier. However, a more plausible explanation, if they do reach below the weir, is that they are preyed upon by the invasive fishes, as seen in other South African streams (Ellender et al., 2018; van der Walt et al., 2016), resulting in extirpation before sampling, and thus they are never captured.

To ensure the eradication of all invasive fishes in the Rondegat River, a second rotenone treatment was applied in 2013 (Slabbert, Jordaan, & Weyl, 2014). This is a common practice for rotenone eradication programmes (Rytwinski et al., 2019), but it also had adverse effects on the native fish populations that had colonized the lower reaches of the Rondegat River, which also coincided with a high rainfall year. One year after the second application, there was a very low probability of colonization downstream from the control section for fiery redfin and Clanwilliam yellowfish and a decrease in colonization for Clanwilliam redfin, suggesting that sites had little to no increase in fish occurrences in 2013–2014. Further, there were higher probabilities of local extinction than of colonization; some pools along the treatment section became unoccupied by native fishes. The rates of change in the occupancy of fishes along the river were $\lambda < 1$, indicative of a decrease in distribution in the treatment section. This also suggests that the fishes from the pristine and control sections colonized the same, although fewer, pools as the previous year within the treatment section, suggesting consistency in recruitment. Fish densities in the treatment section were not significantly different between 2013 and 2014 for Clanwilliam redfin and yellowfish, and they decreased slightly, although not significantly, for the fiery redfin.

The second rotenone application may have adversely affected the treatment section and not released any additional limiting factors, such as smallmouth bass, that affect the distribution of these native fishes. The second rotenone application was planned to mitigate the possibility of some smallmouth bass having survived the first treatment and, thus, ensure eradication (Slabbert et al., 2014). This decision was validated, as one smallmouth bass was later identified by video as being present at one site above the weir prior to treatment in 2013. Although there is merit in this type of management, a balance must be struck between invasive species eradication and endangered species management; however, finding an optimum is difficult (Lampert et al., 2014). There was also higher than average rainfall between the 2013 and 2014 sampling periods (Table 5), causing higher flows (Schulz, 2001). Consequently, juvenile redfin recruits colonizing sites downstream from the pristine and control sections may not have been able to establish or be retained in the treatment section; in other words, they may have been flushed out of the system during this altered flow regime. Modified flow regimes have been shown to affect the distribution and community complexity of stream fishes (Bain, Finn, & Booke, 1988). If this happened, then most redfin juveniles flushed to below the weir would be predated upon by the numerous invasive fishes in the lower section. Conversely, Clanwilliam yellowfish had densities equal to the previous year's densities. Clanwilliam yellowfish is larger than the redfins, perhaps enabling it to resist flushing out of the treatment section. The lack of retention of the redfins within the treatment section would explain the low colonization and higher extinction probabilities. Nevertheless, it is difficult to disentangle the individual or synergistic effects of the

second rotenone treatment and high rainfall on the probabilities of colonization and extinction.

However, rainfall may not be the only factor affecting the population dynamics along the Rondegat River: density-dependent effects could explain some of the variation in the probabilities of colonization and local extinction. There was also no probability of colonization in 2014–2015 for Clanwilliam and fiery redfins, despite average levels of rainfall and an increase in abundance. This suggests that there was no movement along the river, but that the populations were reproducing and growing within pools. Density-dependent effects may be needed to promote dispersal. There are energetic costs to dispersal, growth, and reproduction, and trade-offs between these life-history traits are common (Bonte et al., 2012). The age at maturity of the redfins is approximately 2 years (Ellender et al., 2017). Time to maturation may explain the lack of increased colonization of unoccupied pools by the redfins in 2014–2015, where juveniles that colonized the pools in 2013 from upstream of the Rooidrai waterfall only begin to reproduce in 2015, as dispersal may be contingent on ontogeny and population density, as seen in other fishes (Einum, Robertsen, Nislow, McKelvey, & Armstrong, 2011; Einum, Sundt-Hansen, & Nislow, 2006). As the redfins increased in density in 2015, older individuals capable of dispersing into unoccupied pools in the treatment area, either upstream or further downstream, eventually moved to avoid competition in the denser occupied pools. If this was the case, then there would be an increase in the probability of colonization in 2016, which is shown in the multi-season occupancy models. Furthermore, population abundance remained constant in the treatment section in 2016, a low rainfall year (Table 5). In other words, more pools in the treatment section were occupied but the overall density across the pools in the treatment section was the same, suggesting density-dependent dispersal. Furthermore, in occupied shallower pools, the fishes have higher density, forcing individuals to move into unoccupied pools in the treatment section, thereby increasing the probability of colonization but not density. Other factors, such as predation risk, may also affect the dispersal of the redfins along the treatment section. Shallower pools would increase predation risk by wading and diving predators (Power, 1987), and cyprinids can alter their habitat use to minimize predation by moving to riffles where turbulence decreases visibility or to pools with overhead cover (Allouche & Gaudin, 2001). However, it is not possible to pinpoint which mechanism is responsible for the increased movement and colonization of unoccupied pools based on the information collected from this long-term study.

Overall, both Clanwilliam redfin and Clanwilliam yellowfish seem to have reached a population equilibrium, whereas fiery redfin has not. The top model for Clanwilliam redfin indicates that its occupancy dynamics are at equilibrium within the pristine and control sections, as the occupancy rate of change is around $\lambda = 1$ across the years; however, it is not in equilibrium in the treatment section, fluctuating above and below $\lambda = 1$ across the years. Nevertheless, the model-averaged estimates show that Clanwilliam redfin is more or less in equilibrium throughout the whole river despite variations in the habitat. Conversely, the top model for fiery redfin shows a large increase in the rate of occupancy after the first rotenone treatment throughout the river; but in the following years the rate remained below $\lambda = 1$ until 2016, when it rose above $\lambda = 1$. Similar trends are present in the model-averaged estimates, suggesting that the fiery redfin population in the Rondegat River is not stable and is perhaps more sensitive to fluctuations in habitat variables. Indeed, the endangered fiery redfin densities and occupancy dynamics are much more variable than the other endemic fishes and tend to change with habitat quality, as seen with the removal of invasive trees and presence of invasive species. Slightly different trends are seen for Clanwilliam yellowfish, when in 2014–2015 there was equal probability of colonization and local extinction and occupancy rates of change were estimated to be around 1. This indicates that there was some movement along the river but that the occupancy dynamics are stable and perhaps does not require density-dependent effects to promote dispersal, as abundances remain fairly constant and similar to the control region. Similar to the other two native fishes, there was an increase in colonization in 2015–2016, the low rainfall year, forcing Clanwilliam yellowfish to disperse into other pools to avoid potential intraspecific competition.

Unlike other invasive fish eradication projects that reintroduce native fishes, either from brood stocks or rescues from the same water body (Britton, Davies, & Brazier, 2009; Cochran-Biederman, Wyman, French, & Loppnow, 2015), this study relied on natural recolonization from upstream source populations. This invasive species eradication programme is considered a success, as it eradicated smallmouth bass, and the native fish community has, in a sense, bounced back. According to Cochran-Biederman et al. (2015), there are five steps that should be followed for successful freshwater fish reintroduction, all of which have been achieved by this invasive species management plan. First, the cause of the native fish decline was identified as the presence of smallmouth bass; this study showed that the eradication of this invasive fish was necessary for recolonization by native fishes. Second, the suitability of the habitat was determined to be not fully capable of supporting the full life cycle of the native fishes, as the presence of invasive trees changed the natural habitat; therefore, restoration was necessary, and the invasive trees were removed. Upon regrowth of native vegetation, the density of endangered fiery redfin in the control area increased. Third, the 'reintroduction' of the native fishes was achieved by allowing natural dispersal and recruitment from upstream control and pristine sections of the river, instead of brood stocks or rescues, ensuring that the populations were already adapted to the local environment, an important factor in successful reintroductions (Cochran-Biederman et al., 2015). Further, this study showed that there is continuous recruitment from upstream sources, mimicking repeat introductions from brood stocks in traditional successful reintroduction programmes. The fourth step involves regularly assessing the populations, habitat, and community, and employing adaptive management if necessary; this study confirmed that the fishes have recolonized and continue to occupy the treatment section. Nevertheless, fiery redfin was

identified as still slightly unstable, and further adaptive management may be necessary. The fifth and final step is to confirm project success and implement long-term monitoring, which is continuing in the Rondegat River. This study demonstrated that natural freshwater fish 'reintroduction' can be successful without enhanced restocking from brood stocks or other populations (especially if those resources are unavailable) if there is a source population upstream of the rehabilitated sites. It is important to note that the Rondegat River is unique, as it is relatively small and has natural and artificial barriers to upstream invasions from non-native fishes, increasing chances of downstream repopulation of the river by its endemic fish community.

This study focused on monitoring the occupancy dynamics of three native fishes after the eradication of an invasive fish to assess the recovery of native species over time. It was found that the native fishes quickly colonized the treatment section after rotenone treatment but did not recolonize as quickly after the second treatment. The second eradication coincided with a high rainfall year; hence, it is difficult to disentangle the effects of both these potential stressors. It took about 2 years for the redfins to grow, reproduce, and colonize more pools throughout the treatment area, suggesting that density-dependent factors may have an effect on the recolonization and stability of these IUCN-listed species; the second rotenone treatment may have delayed the full recovery of two native fishes. However, the second rotenone treatment was likely to have been a good strategy, despite the delayed recovery, as one smallmouth bass was detected via video in the treatment section after the first, but prior to, the second treatment. During the low rainfall year, there was increased colonization, indicating that the native fishes were responding quickly to their changing environment. Both Clanwilliam redfin and yellowfish seem to have reached an equilibrium in colonization and local extinction along the river, whereas fiery redfin has not. The stability of the two Near-Threatened fishes throughout the river indicates that the rotenone treatment was effective and that the populations have recovered, whereas the Endangered fiery redfin has yet to reach stability and equilibrium in the Rondegat River.

The eradication of the invasive species alone was not sufficient for full recovery and stability of the native fish community. Other factors may be contributing to the lack of full recovery and stability of the Endangered cyprinid's population. Therefore, additional research on the habitat preferences of the fishes and other threats to the catchment is required to inform further conservation actions, such as habitat restoration within the stream and catchment. Long-term monitoring of the Rondegat River has provided a unique opportunity to study the population dynamics of recovering native fish populations, shedding light on factors that can contribute to long-term population stability and on potential strategies to continue to improve fish population recovery after eradication of invasive species. We recommend that all eradication programmes in any river system undertake long-term monitoring to identify native species recovery and any remaining stressors that may be impeding the desired recovery and stability of a population or community.

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